MORPHOLOGICAL ASPECTS OF SEEDLING ESTABLISHMENT IN FOUR TEMPERATE REGION *PHORADENDRON* (VISCACEAE) SPECIES

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Abstract

Morphological aspects of seedling establishment were studied in four species of the mistletoe genus, *Phoradendron* (Viscaceae). Marked differences occurred between species. In *P. densum* and *P. villosum* the plumular shoot developed as the main shoot of the plant, whereas in *P. juniperinum* the plumular shoot failed to develop in about 10% of seedlings. When the plumular shoot failed to develop a nonplumular seedling shoot displaced the original seedling axis to a lateral position near the base of the developing nonplumular shoot. The undeveloped seedling axis may remain attached and living for several years. In *P. californicum* the plumular shoot never developed in two of the populations studied, but did develop in a small percentage of individuals in a third population. In both species nonplumular shoots developed from a mass of tissue, termed the haustorial cushion, that forms immediately beneath the holdfast. A haustorial cushion was also observed in *P. densum*, but the shoot buds that formed on the cushion rarely developed into shoots. Cotyledon characters also varied between species, but in all four species the small cotyledons were persistent. Contrary to earlier reports, the cotyledons do not later develop into foliage leaves. In agreement with Kuijt (1990) we regard the cryptocotylar condition observed in *P. californicum* and, on rare occasion, in *P. juniperinum*, both squamate species, to be advanced. The morphological, ecological and evolutionary implications of these observations are illustrated and discussed.

Phoradendron and six closely related genera comprise the mistletoe family, Viscaceae. It has recently been suggested that the seven viscoid genera be transferred to the Santalaceae (APG 1998). The large genus *Phoradendron* is broadly divided into two subgroups, based on the presence or absence of scale-like appendages, the cataphylls (Wiens 1964). The acataphyllous species are predominantly northern in distribution, and all but one of the U.S. species are from this group. Monographs of the genus include those by Trelease (1916) and Wiens (1964) (acataphyllous species only). A revision of the entire genus is now in progress (Kuijt personal communication). Ashworth (2000) has analyzed phylogenetic relationships in the tribe Phoradendreae, which includes both *Phoradendron* and the sympatric and morphologically similar genus, *Dendrophthora*.

The seven viscacean genera are considered to have relatively uniform seedlings (Kuijt 1982), except for the genus *Arceuthobium*. Typically, the elongating root axis is the first organ to emerge from the seed (Calvin 1966; Kuijt 1969; Tubeuf 1923). As the tip of the root contacts the host branch, a disc-shaped holdfast is formed. Subsequently, the seedling becomes erect, with its cotyledons and shoot tip still enclosed within the fruit mass. Eventually the fruit vestiges are shed and the elongating plumular shoot emerges. Developed seedlings of both *Viscum album* L. (Tubeuf 1923)

and *Phoradendron macrophyllum* (Engelm.) Cockerell (Calvin 1966) have an elongate hypocotyl, two small cotyledons and a plumular shoot. While the first aerial shoot is usually plumular in origin, shoots may also arise from the haustorial disc region and/or from the endophytic system, particularly when the plumular shoot is damaged or lost (York 1909). Information on seedlings of the traditional santalacean mistletoes is sparse (Kuijt 1990).

The pattern of seedling establishment in the highly specialized genus *Arceuthobium* is strikingly different than that described for *Viscum* and *Phoradendron*. In *Arceuthobium* the cotyledons are only rudimentary, and the shoot apex is poorly developed (Cohen 1963). At germination epicotylar growth is suppressed in favor of endophytic establishment (Kuijt 1969). All aerial shoots are root-borne, arising from the endophytic system two or more years after the initial infection (Hawksworth and Wiens 1996). *Phoradendron californicum* Nutt. is reported to have a pattern of establishment similar to that of *Arceuthobium* in that, like *Arceuthobium*, aerial shoots are said to arise exclusively from the endophytic system (Kuijt 1989). In *Viscum minimum* the embryonic shoot apex aborts, and the initial seedling shoots arise from the endophytic system or shoot buds that form on the holdfast or directly below it (Kuijt 1986). The shoot apex of *P. macrophyllum*, a large-leaved species, appears to be more highly developed than that of *Arceuthobium* (compare Cohen 1963, fig. 3, with Calvin 1966, fig. 9). Major changes from the usual

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sequence of seedling growth, such as reduction or suppression of embryonal apical differentiation, seem to be an evolutionary trend in parasitic flowering plants (Teryokhin and Nikiticheva 1982).

For mistletoes in general an insufficient data base exists on seedling structure (Kuijt 1982). This lack of basic information can lead to misinterpretation of life cycle sequences important to physiological, developmental, and taxonomic determinations. During another study (Calvin et al. 1993) we noted a number of unusual seedling features in *P. juniperinum.* This observation, coupled with Kuijt's (1982) comments on the paucity of information on mistletoe seedlings in general, prompted this study. Three additional species of *Phoradendron* were included to provide a comparative dimension to the study and to broaden its focus. Our field and laboratory studies indicate that a greater variation in seedling morphology exists within the genus than has been reported.

Materials and Methods

The four species of *Phoradendron* chosen for this study were: *P. californicum* (desert mistletoe), *P. densum* Trel. (dense mistletoe), *P. juniperinum* A. Gray (juniper mistletoe), and *P. villosum* (oak mistletoe). For *P. juniperinum,* the primary focus of the study, several hundred seedlings were examined. Fewer specimens (100–200) were analyzed for each of the other species studied. More than one population was utilized for 3 of the species, as indicated below. The 4 species studied occur at the northern limit of the *Phoradendron* range. Two of the species, *P. californicum* and *P. juniperinum,* are squamate; that is, their leaf blades are scale-like. *Phoradendron densum* has small leaves, and *P. villosum* has leaves of medium size (as compared to *P. macrophyllum*).

Specimens of the four *Phoradendron* species were collected at intervals during the years 1984–1987. The materials of *P. californicum* were collected in proximity to Mesquite, NV, Oatman, AZ, and on the Cabezon Indian Reservation near Indio, CA. The host trees were primarily *Prosopis,* but specimens were also collected from *Acacia, Cercidium* and *Larrea. Phoradendron densum* was collected 6.5 miles downstream from the J. C. Boyle Powerhouse in Klamath Canyon, OR, and in the vicinity of Weed and Henley, CA. The host tree was *Juniperus. Phoradendron juniperinum* was collected in and near Bend, OR, also growing on *Juniperus. Phoradendron villosum* was collected in two widely separated localities: near Corvallis, OR, and 30 miles east of Red Bluff, CA, along State Highway 36. *Herbarium* specimens of the four species studied are deposited in the Portland State University Herbarium (HPSU). For all species, collected specimens were brought to the laboratory and examined while fresh, using a Zeiss dissecting microscope. Some specimens were preserved in alcohol for further study. Description of gross shoot morphology centered on the nature of the cotyledons (number, size, fused or free, persistence, visibility), the origin of aerial shoots (plumular, haustorial disc region, endophytic system), the fate of aerial shoots, internode extension, and length of the hypocotyl.

In this study three categories of aerial shoots are recognized: 1) *Plumular shoots,* arising from the shoot pole of the embryo; 2) *Nonplumular seedling shoots,* arising from the haustorial disc or cushion region; and, 3) *Root-borne shoots,* arising from the endophytic system. Nonplumular seedling shoots probably represent a type of root-borne shoot; but they are segregated here since a major focus of this report is on the contrasting origins of aerial shoots in the species studied. Further, since the morphological nature of the holdfast and cushion regions remains problematic, a distinction is justified.

Results

In the Bend, OR, area the fruits of *Phoradendron juniperinum* reach maturity in early winter. Several bird species feed on these fruits and void seed on nearby host branches (Fig. 1). Shortly thereafter germination begins. In *P. juniperinum* (Figs. 1–12) and the other *Phoradendron* spp. examined the radicle is the first structure to emerge from the seed (Fig. 1). The specimen shown was collected in mid-May and reflects the slow but continuous growth of the green hypocotyl-root axis. Eventually the root tip reaches a penetration site, which is typically, but not always, beneath a scale leaf, and form a holdfast (Fig. 2). Throughout this stage the cotyledon tips remain more or less embedded within the endosperm, which is in turn covered by the sclerophyllous "seed" coat (Fig. 2). As growth continues, the seedling becomes erect, shedding the remnants of the endosperm, and the plumular shoot develops (Fig. 3).

At this stage of seedling growth striking differences between seedlings become evident. In many seedlings an expanded region of tissue, here designated the haustorial cushion, develops beneath the holdfast raising it above the host surface (Fig. 4). Of 254 seedlings studied for this feature 52% developed a cushion. Typically, 2–4 vegetative buds arise on the cushion (Fig. 4), but as many as 11 were observed. These buds may remain dormant for a time (Fig. 4) or initiate shoot growth almost as soon as they appear (Fig. 5). Seedlings that failed to form a cushion did not develop nonplumular seedling shoots at the initial infection site. Root-borne shoots may develop later, however, directly from the endophytic system. The development of shoots from the endophytic system is a common phenomenon in some viscacean genera and has been observed by several workers (Bray 1910; Cannon 1901; Kuijt 1969; York 1909).

In approximately 20% of specimens studied,
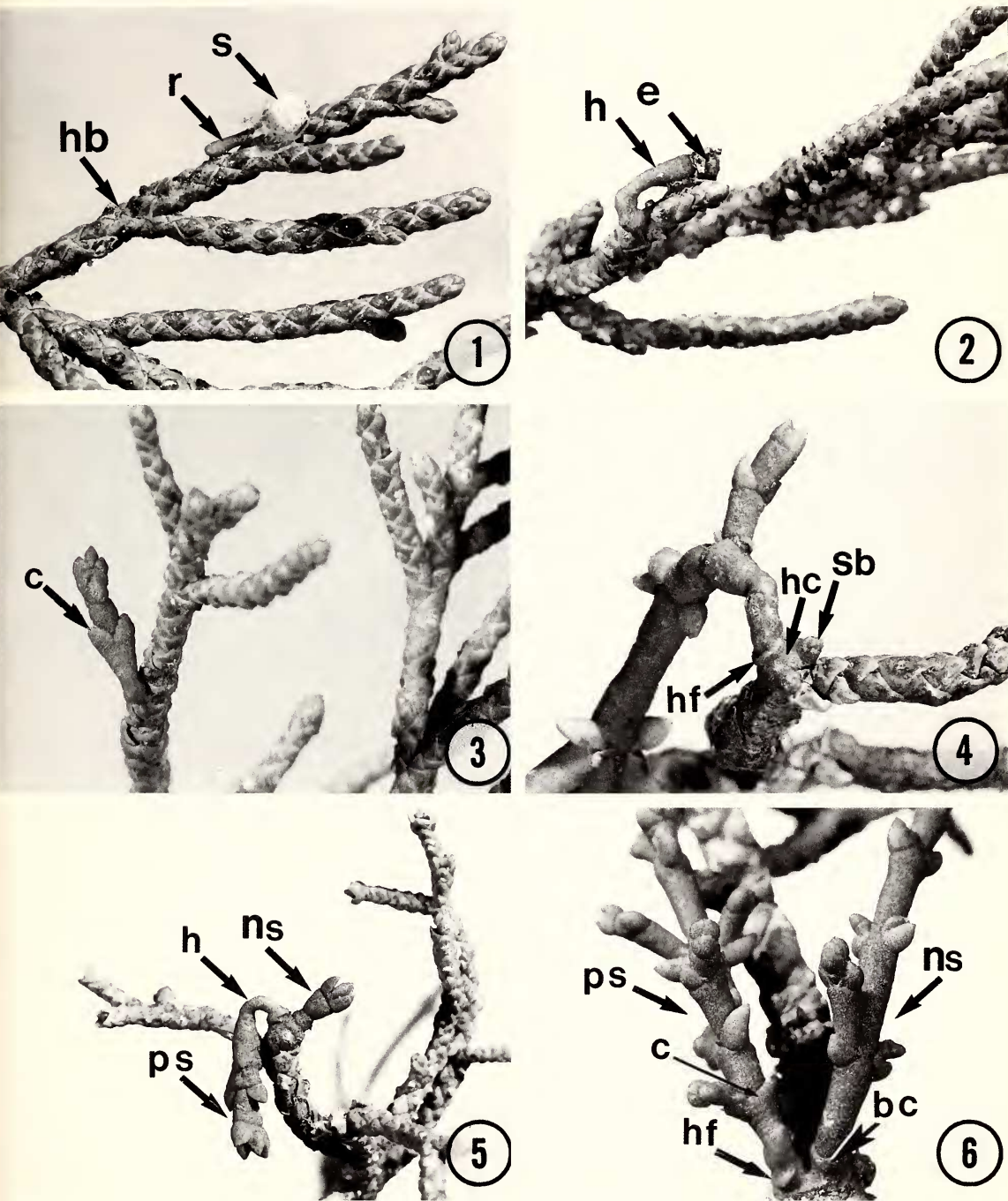
FIGS. 1–6.   *P. juniperinum.* Fig. 1, germinating seed, s, with elongate hypocotyl-root axis, r. Fig. 2, seedling with elongate hypocotyl, h, and holdfast label? Fig. 3, seedling with cotyledons, c, and plumular shoot. Fig. 4, young plant showing holdfast, hf, haustorial cushion, hc, and vegetative shoot bud, sb. Fig. 5, seedling with curved hypocotyl, prominent holdfast, young plumular shoot, ps, and developing nonplumular shoot, ns. Fig. 6, young plant with well-developed plumular and nonplumular seedling shoots; note basal cup, bc, present at base of nonplumular seedling shoot; endosperm remains, e; host branch, hb. All ×1.

nonplumular seedling shoots originating on the haustorial cushion equaled (Fig. 6) or surpassed plumular shoots in size by the time the latter had five extended internodes. Nonplumular shoots can be identified by a basal, cup-like structure, presumably the lowermost leaf pair. Plumular shoots, in contrast, have a holdfast, a hypocotyl and cotyledons (Fig. 6).

A particularly interesting feature observed in some *P. juniperinum* seedlings is the virtual absence of growth from the plumular apex. This phenomenon was noted in about 10% of the seedlings examined. In this event, the growth of nonplumular shoots displaces the original seedling to a lateral position near the base of the developing nonplumular seedling shoots (Figs. 7–9). The remnants of the initial seedling are persistent and have been seen on infections in which developing shoots had ten or more extended internodes. When first observed these small, undeveloped "basal" seedlings were interpreted to be autoparasites, but as developmental stages were examined the true nature of these seedling structures became evident.

Nonplumular seedling shoots often appear more vigorous than shoots developing from the embryonic shoot apex. This vigor may be related to several factors. Frequently nonplumular shoots have a darker green color than plumular shoots (Fig. 9), possibly reflecting a higher content of chlorophyll. A constriction, not seen in other shoots, is often evident in the hypocotyl region of plumular shoots immediately above the holdfast (Fig. 10). Additionally, extreme curvature of the hypocotyl can occur in this region (Fig. 11). These features may diminish the quality and quantity of the vascular connection between shoot and root. Constriction and/or curvature may also represent a weak point, since seedlings broken off in this region were observed in the field.

Phoradendron juniperinum generally has two cotyledons (Fig. 3) although the number ranges from one to three. Usually the cotyledons are free and spreading; that is, plants display phanerocotyly (Figs. 3, 6). In some cases the cotyledons may be partially or wholly fused along one edge; rarely they are fused to such an extent that the demarcation between the individual cotyledons is difficult to discern (Fig. 12). The cotyledons display a set of morphological characteristics that distinguishes them from subsequent leaves. First, their extreme tips (approximately 1 mm) are seen to be pointed and chlorotic upon removal of the endosperm. Later the points appear brown and withered. These minute tips are nearly always present, and can be seen when cotyledons are examined closely. Second, the cotyledons join smoothly and without interruption with the hypocotyl region (Fig. 3), whereas the subsequent scale leaves often have a definite line of demarcation at their junction with the stem (sl in Fig. 9). Third, the cotyledons are not deciduous, whereas in species with foliage leaves (but not in

P. juniperinum) the latter are deciduous. Although the shape of cotyledons changes as stem diameter increases, they can still be recognized on specimens such as that seen in Figure 12, which has over 20 extended internodes. Using these criteria the presence of cotyledons can be used to distinguish between plumular and nonplumular shoots in the field.

Phoradendron densum (Figs. 13–18) follows closely the sequence of events described for early seedling growth of *P. juniperinum*. Following germination and holdfast formation, the seedling becomes erect (Fig. 13). A haustorial cushion may also form, but not as commonly as in *P. juniperinum*. Of 121 specimens examined, 37% had a haustorial cushion. Generally one or two shoot buds are initiated on the cushion, but 90% of these had not developed into shoots even after seven extended internodes were visible on the plumular shoot. It was noted, however, that all buds produced shoots in the six cases where the original seedling had been damaged by herbivory or mechanical injury. This species frequently produces root-borne shoots directly from the endophytic system, and large clusters of these shoots are found at varying distances from the initial infection site. In none of the plants examined did we observe arrested plumular shoot growth as illustrated in Figures 7–9 for *P. juniperinum*.

The cotyledons of *P. densum*, typically two or three in number, display the distinct morphological features described for *P. juniperinum* (Fig. 14). Fusion of the cotyledons is common, occurring at their tips (Fig. 15), along their margins (Fig. 16), or a combination of these (Fig. 17). In any event, the cotyledons do not appear to enlarge very much and remain smaller, although somewhat more succulent, than subsequent foliage leaves. With continued lateral expansion of the main stem, the cotyledons may assume a position perpendicular to the stem axis, and they persist even after foliage leaves above them are lost (Fig. 18). As in *P. juniperinum*, the presence of cotyledons is a reliable indicator of plumular shoots.

Seedling development in *P. californicum* (Figs. 19–24) differs from that of both *P. densum* and *P. juniperinum*. Upon germination the extending radicle, which is distinctly reddish in color, forms a holdfast from which the endophyte is established (Fig. 19). Seedlings may then become erect with respect to the host branch (Fig. 19) or remain in the same plane as the host branch (Figs. 20–22). At about the same time a thin to somewhat thickened haustorial cushion forms immediately below the holdfast, elevating the holdfast above the branch surface (Figs. 20, 22). From the cushion region an average of seven, but as many as 20, shoot buds are formed (Fig. 23). When a large number of shoot buds are formed, they may be present around the entire periphery of the cushion, eventually forming shoots that radiate outward in
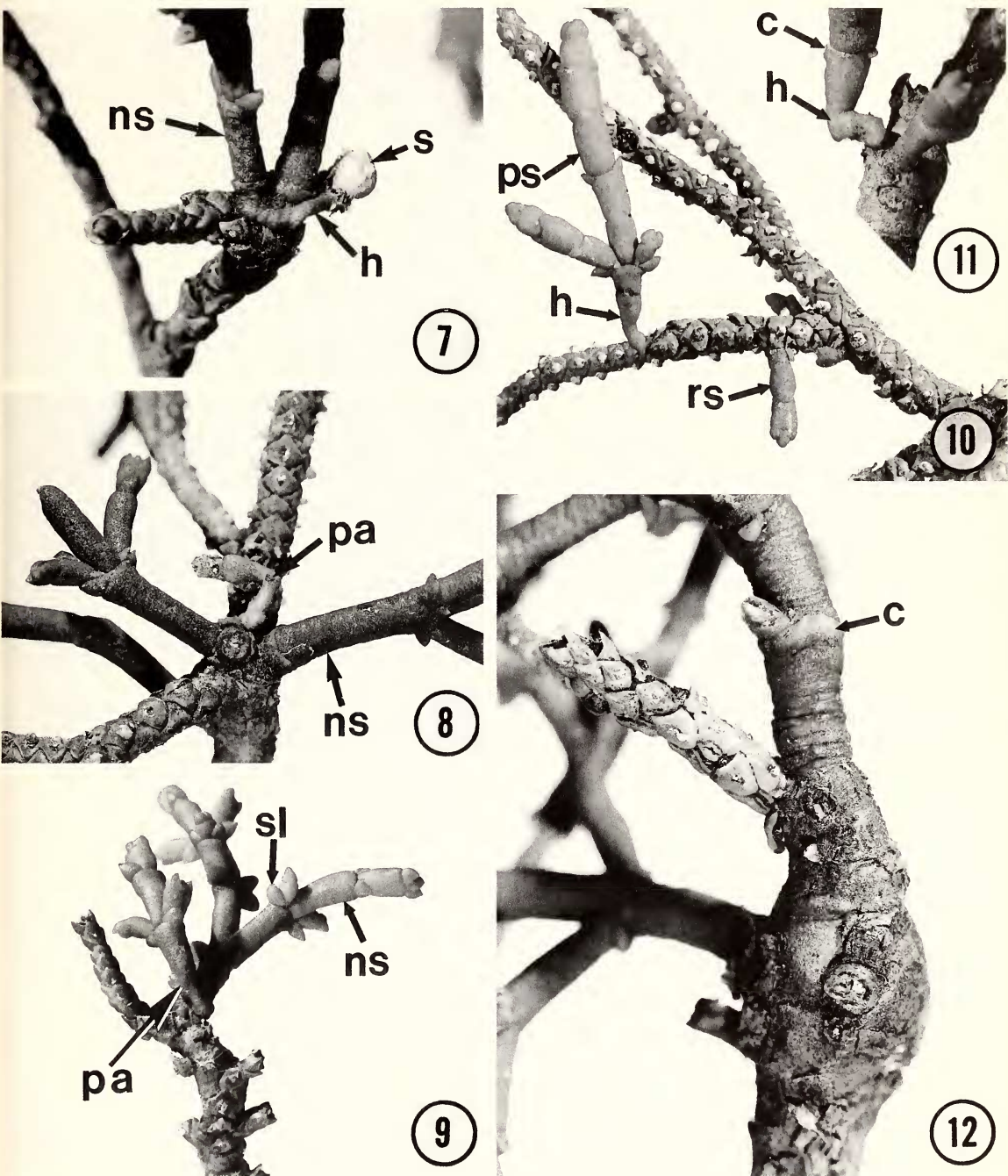
Figs. 7–12.   *P. juniperinum.* Fig. 7, nonplumular seedling shoot, ns, with undeveloped plumular axis at base as evidenced by seed, s, with developed hypocotyl-root axis, h. Fig. 8, plant with 2 nonplumular shoots and basal, undeveloped plumular axis, pa. Fig. 9, young plant with developing nonplumular shoots and basal plumular axis. Fig. 10, seedling with developed plumular shoot, ps; note constricted hypocotyl and adjacent root-borne shoot, rs. Fig. 11, portion of young plant showing minute cotyledons, c, and contorted hypocotyl. Fig. 12, older plant; fused cotyledons still visible; scale leaf sl. All ×1.

all directions from the initial infection site (Fig. 24). Regardless of their number and distribution, the vast majority of vegetative buds develop, resulting in infections having thick clusters of shoots. Shoots may also arise from the endophytic

system, particularly when the initial infection site is at a node.

In all but one population of *P. californicum* 100% of plumular shoots failed to develop. However, the original seedling remained, often for
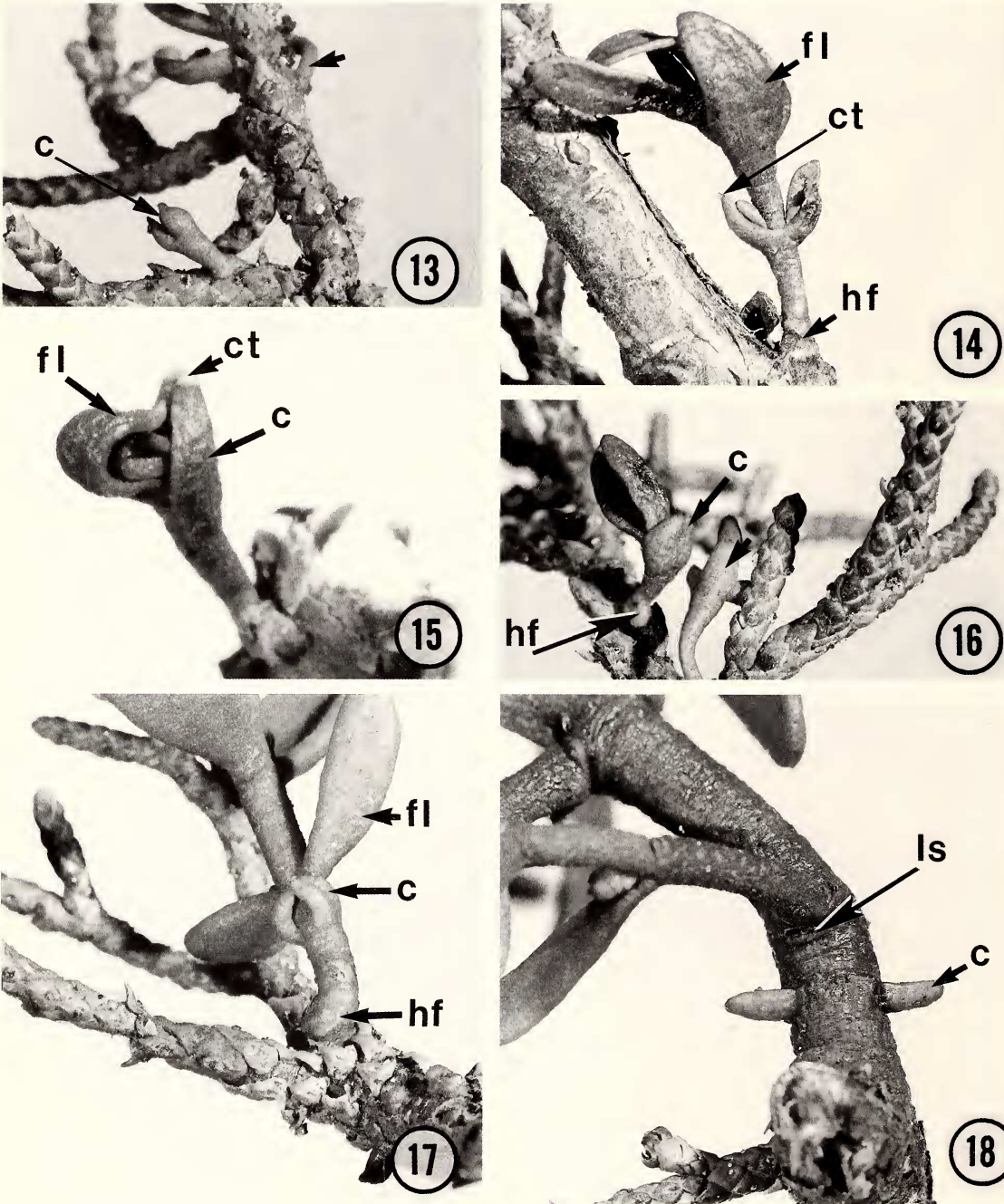
FIGS. 13–18. *P. densum.* Fig. 13, seedling with cotyledons, c; note second seedling at unlabeled arrow. Fig. 14, older seedling with succulent cotyledons and foliage leaves, fl. Fig. 15, seedling with cotyledons united at tip, ct, and emergent foliage leaves. Fig. 16, two seedlings, seedling at left has fused cotyledons and emergent foliage leaves. Fig. 17, seedling with three cotyledons fused both at tips and margins. Fig. 18, older plant with persistent cotyledons, note leaf scar, ls, at adjacent node; holdfast, hf. All ×1.

years, as a usually living hypocotyl-root axis in amongst the developing nonplumular seedling shoots (Fig. 24). In some cases the elongate hypocotyl-root axis becomes erect, and remnants of the endosperm may remain visible, obscuring the cot-

yledons (Fig. 22). Although not always readily visible, the location of the failed plumular shoot clearly identifies the initial site of infection. In the Cabezon Indian Reservation population, in contrast, the plumular shoot had developed in 5 of 17 newly
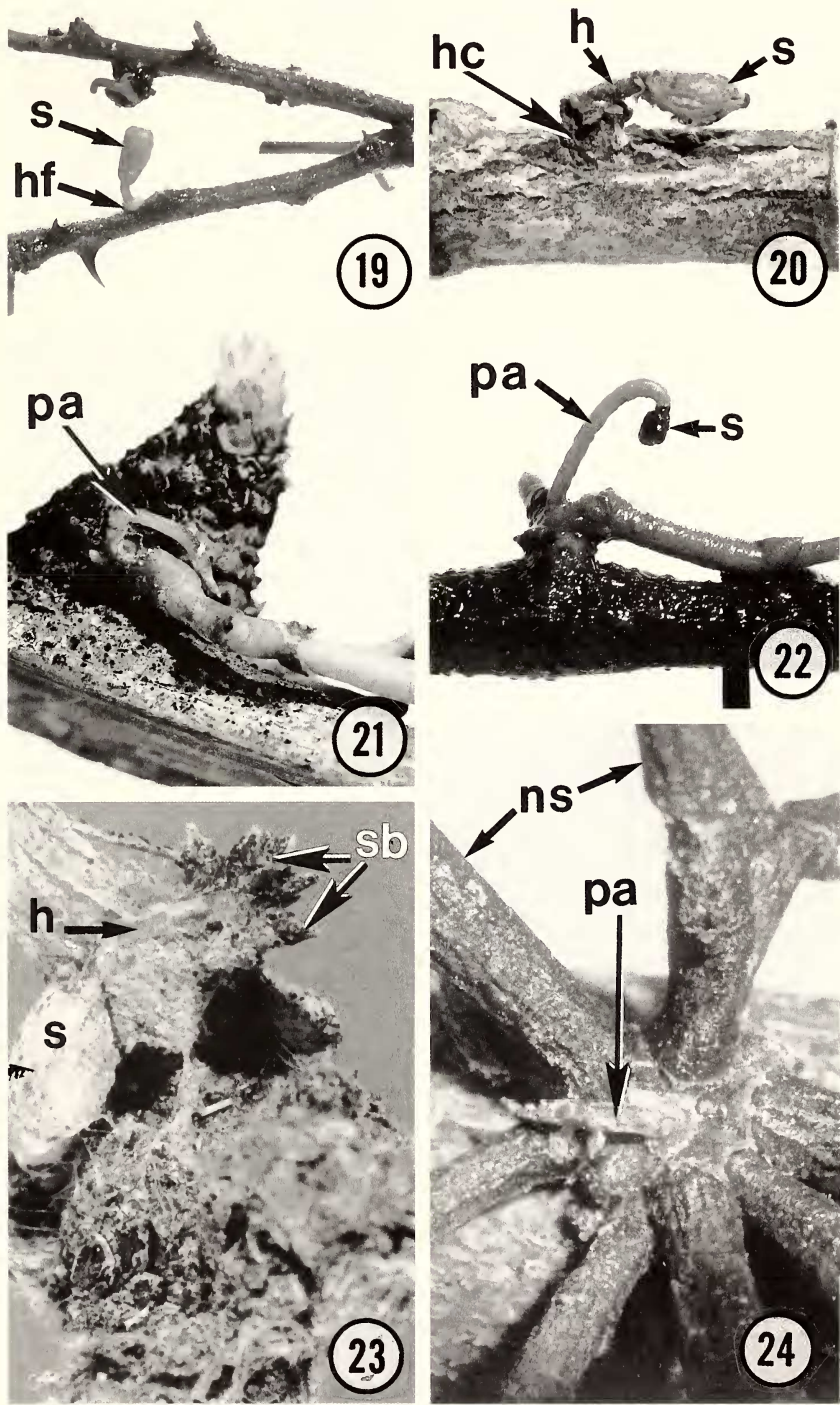
FIGS. 19–24.   *P. californicum.* Fig. 19, germinated seed, s, with holdfast, hf. Fig. 20, germinated seed that has entered host tissue; note elevated haustorial cushion, hc, beneath holdfast. Fig. 21, young plant with undeveloped plumular axis, pa, at base of nonplumular shoot. Fig. 22, young plant with erect, undeveloped plumular axis at base of nonplumular shoot. Fig. 23, germinated seed with elongate hypocotyl, h, and several vegetative shoot buds, sb, radiating outward from the haustorial cushion. Fig. 24, older plant with seven nonplumular shoots, ns; note plumular shoot axis at center of radiating shoots. All ×1.

established seedlings examined. In these seedlings the endosperm mass had been shed and the cotyledons were clearly visible. In size and form, the cotyledons resembled those of *P. juniperinum*. All of the seedlings had two cotyledons, and in none were the cotyledons fused.

Seedling establishment in *P. villosum* resembles closely establishment events described previously for *P. macrophyllum* (Calvin 1966). Dispersed seed lie flat upon the host branch. At germination the elongating hypocotyl-root axis makes contact with the host branch and a holdfast is formed (Fig. 25). Subsequently seedlings become erect (Figs. 26, 27) and the plumular shoot begins its development. In all seedlings and juvenile plants examined two separate cotyledons were evident. As in the other species described herein the cotyledons were small with brownish, pointed tips. Also, the cotyledons were persistent, remaining on the plant long after later-formed leaves had abscissed (Figs. 26, 27). Finally, as in the other species, the internode immediately above the cotyledons frequently showed little or no elongation (Fig. 26). In none of the more than 25 seedlings examined was a haustorial cushion evident, and in none of the specimens were shoot buds present at the infection site. Presumably, root-borne shoots can develop from the endophytic system of *P. villosum*, as occurs in other *Phoradendron* species, but none were observed in the specimens examined. Instead, younger shoots were seen to have two small but persistent cotyledons (Fig. 27).

The seedling establishment events described above for four *Phoradendron* species share features in common with seedling establishment in other viscoid genera, as well as in *Tupeia*, a member of the Loranthaceae. In Figure 28 is shown a seedling of *Viscum rotundifolium* collected in South Africa. Visible are the holdfast, elongate hypocotyl, and two small, persistent cotyledons with pointed ends (shown enlarged in Fig. 29). Note also that the internode directly above the cotyledons did not elongate, as is common in *Phoradendron*. In Figure 30 is shown a seedling of *Notothixos subaureus* collected near Wisemans Ferry, New South Wales, Australia. The seedling has a holdfast, an erect, elongate hypocotyl and two minute cotyledons. Immediately above the cotyledons are two shoots. It appears that both of these shoots arose from axillary buds following injury to the main, plumular shoot. Finally, more than 100 seedlings of *Tupeia antarctica*, growing on tree lucerne on the Banks Peninsula near Christchurch, New Zealand, were examined for seedling characters. Remarkably, more than one third of these seedling showed small, arrested plumular shoots near the base of their developed nonplumular seedling shoots, a situation almost identical to that illustrated for *P. juniperinum* (Figs. 7–9) and *P. californicum* (Figs. 21–24).

DISCUSSION

Dispersed and germinating seed of the *Phoradendron* species studied lie flat on the host branch; that is, their smallest dimension is perpendicular to the branch surface. A similar placement is found in the viscoid genera *Arceuthobium* (Hawksworth and Wiens 1996), *Notothixos* (McLuckie 1923) and *Viscum* (Salle 1983; Kuijt 1986). Dispersed and germinated seed of many loranth genera also lie flat against the host branch (Polhill and Wiens 1998; McLuckie 1923; C. L. Calvin personal observation). This stands in marked contrast to the dispersed and germinating seed of the loranth genera *Alepis* and *Peraxilla* which stand on end (Ladley et al. 1997). In these genera the root tip points away from the host branch, and the elongating hypocotyl-root axis curves 180 degrees to contact the host. This contrasting orientation apparently relates to the distribution of viscin in fruits. In both *Alepis* and *Peraxilla* the viscin is positioned in a ring near one end of the seed (Ladley et al. 1997), whereas in the viscoids studied the viscin is dispersed more evenly around the seed.

The formation of a haustorial cushion is described for three of the species studied. This cushion arises at the base of the holdfast and is the site of origin of nonplumular seedling shoots. In *P. juniperinum*, which has the most pronounced cushion, its development may raise the holdfast well above the surface of the host branch. Kuijt (1986) noted that in *V. minimum* seedlings aerial shoots may also arise from directly beneath the attachment disc, as well as from the margin of the disc. York (1909) found that in *P. macrophyllum* "the aerial shoots which are first formed usually arise from buds, which develop on the attachment disc. . . ." In the present study shoot buds were not seen to arise on the attachment disc (holdfast), but rather on the cushion of tissue formed directly beneath the holdfast. The shoots of *V. minimum* that arise beneath the holdfast (Kuijt 1986) presumably also arise from a cushion-like region.

The first aerial shoots of *Phoradendron* seedlings have generally been regarded as being plumular in origin (Cannon 1901; York 1909; Calvin 1966). In the present study the initial shoots of *P. densum* and *P. villosum* were exclusively plumular in origin, whereas those of *P. californicum* were almost entirely nonplumular. Seedling shoots in *P. juniperinum* were either plumular or, somewhat less commonly, nonplumular in origin. Where plumular shoot growth is arrested shoots arise from shoot buds initiated on the haustorial cushion formed beneath the holdfast. Additionally, root-borne shoots may be formed in proximity to the infection site (see rs in Fig. 11), particularly in *P. californicum*. These contrasting patterns of shoot origin represent a greater diversity than previously recognized. The situation in *P. californicum* approaches that in *Arceuthobium* spp. (Cohen 1963; Hawksworth and
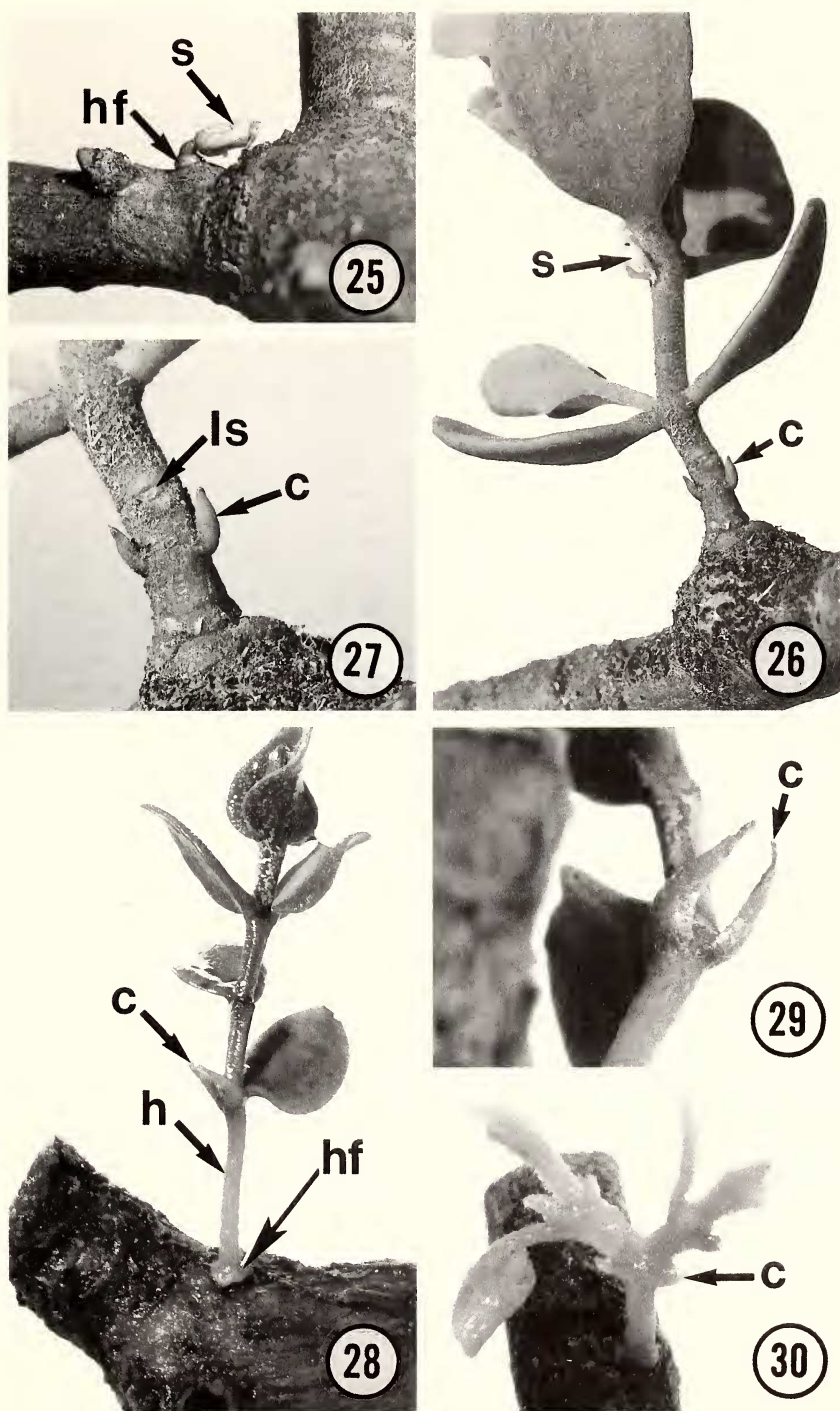
FIGS. 25–30.   *P. villosum* (Figs. 25–27), *V. rotundifolium* (Figs. 28, 29) and *N. subaureus* (Fig. 30). Fig. 25, germinated seed with well developed holdfast, hf. Figs. 26, 27, seedling with two cotyledons; note leaf scar, ls, above and directly opposite cotyledons. Figs. 28, 29, young plant with elongate hypocotyl-root axis, holdfast and free cotyledons (one of the two leaves attached at the node directly above cotyledons was removed to enhance visibility of cotyledons). Fig. 30, seedling with two minute cotyledons and small plumular shoot; cotyledon, c, hypocotyl-root axis, h, seed mass, s. All ×1.

Wiens 1996) and in *Tristerix aphyllus* (Mauseth et al. 1984) where the initial shoot and all succeeding shoots are root-borne. In *P. californicum*, however, the first aerial shoots arise from an aerial portion of the seedling, not from the endophytic system as has been reported (Kuijt 1989). In *Arceuthobium* and *T. aphyllus*, on the other hand, the initial shoots arise from the endophytic system and do not appear for some time after penetration of the host branch; about two years in *Arceuthobium* spp. (Hawksworth and Wiens 1996).

The cotyledons of the *Phoradendron* species studied varied in both number and form. Most seedlings of *P. juniperinum* had two cotyledons, but a few had either one or three. In *P. densum* either two or three cotyledons were present, whereas in *P. villosum* all seedlings had two cotyledons. The few plumular shoots of *P. californicum* observed in the Cabezon population also had two cotyledons. The cotyledons of *P. densum* were the largest and most succulent in appearance, those of *P. juniperinum* and *P. villosum* were intermediate in size and those of *P. californicum* the smallest. Fused cotyledons were common in *P. densum*, but rare or absent in the other *Phoradendron* species. Observations of earlier workers on the fate of cotyledons are in conflict. Bray (1910) states that in *P. macrophyllum* the cotyledons become erect and slowly expand as the first pair of green leaves. York (1909), on the other hand, states that the cotyledons either wither or become slightly enlarged but never form foliage leaves. Our observations are more similar to those of York. Of interest, in all 4 species the cotyledons were persistent, as are the scale leaves of the squamate species. In contrast, the subsequently formed foliage leaves of *P. densum* and *P. villosum* are deciduous. Persistent cotyledons that do not develop into foliage leaves are considered unusual, and Sporne (1974) cites only two examples of this phenomenon, both in the family Gesneriaceae.

Phoradendron densum and *P. villosum* were consistently phanerocotylous. The vast majority of specimens of *P. juniperinum* were also phanerocotylous, but in occasional specimens, such as those shown in Figures 7 and 8, the cotyledons never emerge. In contrast, in only a single population of *P. californicum* were seedlings observed in which the cotyledons were visible and spreading. It is probable that the ancestor of the viscoids was phanerocotylous, as are the majority of modern viscoid species. In agreement with Kuijt (1990) we regard the cryptocotylar condition observed in highly specialized, squamate species of *Phoradendron*, illustrated here by *P. juniperinum* and *P. californicum*, to be advanced. Cryptocotyly is regarded by some as the ancestral germination pattern in angiosperms as a whole (Gifford 1991).

The four *Phoradendron* species examined show a progressive reductional trend in leaf size. Leaves of *P. villosum* are of intermediate size (compared

to those of *P. macrophyllum*, for example), those of *P. densum* are small and those of *P. juniperinum* and *P. californicum* are reduced to scales. The four also display reductional trends in seedling development. In this series plumular shoots give way to nonplumular seedling shoots developing on a haustorial cushion, and phanerocotyly is replaced by cryptocotyly. This trend is carried even further in *Arceuthobium* species. In all members of this genus aerial shoots are root-borne, and neither plumular shoots nor nonplumular seedling shoots are ever formed (Hawksworth and Wiens 1996). The significance of these reductional trends is difficult to ascertain. One possible advantage is the formation by seedlings of a larger number of seedling shoots—a sort of tillering—at an early age through the formation of shoot buds either on the attachment disc or on the proliferative tissue formed beneath the attachment disc. Also, as noted earlier, nonplumular seedling shoots frequently appear more vigorous than plumular shoots when both occur together in a seedling. Finally, species capable of forming nonplumular seedling shoots and/or root-borne shoots have much greater vegetative and reproductive versatility than those relying solely on plumular shoots.

Reduction in or suppression of plumular shoot growth is common in the viscoid mistletoes. It is illustrated here for *P. juniperinum* and *P. californicum*, and described elsewhere for *V. minimum* (Kuijt 1986) and *Arceuthobium* (Kuijt 1969; Hawksworth and Wiens 1996). Reduction in or suppression of plumular shoot growth also occurs in some Loranthaceae. In the New World loranth *T. aphyllus*, all seedling aerial shoots are reported to be root-borne (Mauseth et al. 1984), a condition analogous to that in *Arceuthobium* species. The frequent absence of plumular shoot growth is also reported here for the monotypic New Zealand loranth, *Tupeia antarctica*. It is probable that the suppression of plumular shoot growth occurs to a lesser or greater degree in other genera of viscoids and loranths as well. In *Phoradendron* and other viscoids the suppression of plumular shoot growth is positively correlated with the squamate habit. It is interesting that the suppression of plumular shoot growth is common in species that are considered specialized within their respective clades when it represents a basic growth pattern.

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